THE DEVELOPMENT OF THE WING OF STERNA WILSONII.

By Virgil L. Leighton.

Although various students have investigated the structure and the development of the wing of the bird, many points still remain unsettled, and prominent among them, the relations of the carpal elements, the number of digits present and the comparison of these digits with those of the normal pentadactyl manus. Professor J. S. Kingsley suggested to me to attempt the solution of some of these problems and the studies detailed below were carried out in the Biological Laboratory of Tufts College under his direction. To him I owe the material—embryos of various stages of Wilson's tern, *Sterna wilsonii* from the Island of Penekese, Mass.—which formed the basis of my work.

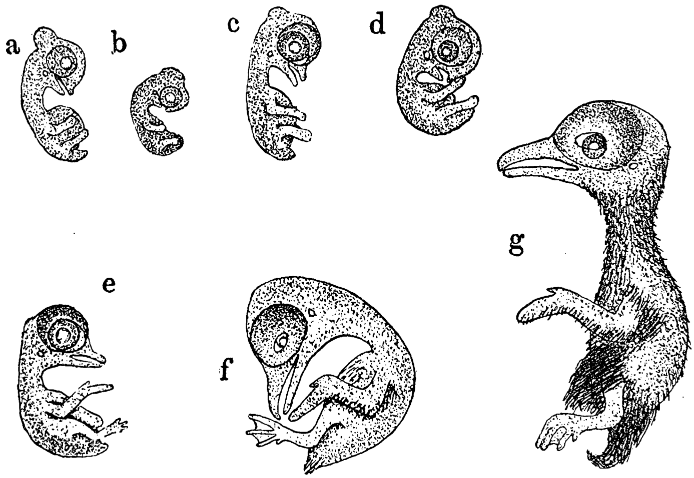
The alcoholic material was studied both in toto by clearing with oil of clove, and by means of serial sections. The latter proved far preferable and much more dependence can be placed upon results obtained in this way, especially with the younger embryos than by the more common methods of dissection and clearing in essential oils. The figures of structural details which illustrate the paper were obtained from reconstruction projections of the sections and are magnified twenty diameters. I am not able to state the ages of the various embryos, but this is a matter of little importance since the approximate development can readily be made out from the figures of the various stages, each natural size. The numbering of the separate stages is entirely arbitrary.

I might state here, incidentally, that I have also studied to some extent the foot of the tern and I find in it, as has already been pointed out by other observers, (Miss Johnson, Studer, W. K. Parker and others) a fifth metatarsal present.

Stage I, (Fig. 1).

At this stage (fig. a) the principal elements of the wing are becoming differentiated. The radius and ulna are entirely

cartilaginous, except a small portion at their distal ends where they are least developed. In the proximal row of carpals are two masses of rapidly forming cartilage (radiale and ulnare) each of which appears to have two centers of chondrification.



The larger (the radiale, *re*) is almost divided into two parts; of these the larger and outer one is somewhat triangular in shape and is fitted upon the distal end of the radius, the smaller and inner one is nearly circular and is contiguous to the inner margin of the distal end of the ulna. The ulnare is composed of two oval centers, the proximal being about half the diameter of the distal one, thus giving the whole element a wedge-shaped appearance with its narrow end passing just outside the outer margin of the ulna.

The distal carpals are represented only by a thickening of tissue, or "procartilage" of Parker, showing as yet no differentiation into separate elements. There are *four* radiating digits represented for the most part by "procartilage," but metacarpals II[1] and IV are becoming cartilaginous at their proximal ends and metacarpal III is two-thirds cartilage.

STAGE II, (FIG. 2).

This stage (fig. b) is but slightly more developed than the last. The cartilage is a little more pronounced, and digits II,

[1]For the numbers to be given to the digits, see below.

III and IV have become longer, III and IV being segmented. The fourth digit has become free from the central mass, and more nearly approximated to digit IV. In the distal carpal series there are two masses of cartilage: on the radial side a mass which represents the combined carpales II and III, and on the side of the ulna carpale IV, an oval mass contiguous proximally to the distal lobe of the ulnare and distally to its own metacarpal.

Stage III, (Fig. 3).

In this stage (fig. c) there are several things to be noted. The spreading of the digits is not so great and the whole manus is beginning to flex towards the ulnar side, thereby displacing some of the carpals from their normal position. The elements are now all perfectly distinct, the radiale has entirely lost its bibobate appearance, and is now of an irregular shape, touching the radius and ulna and the approximate surface of the conjoined carpales II and III. The ulnare is now entirely outside the ulna, but, what seems most remarkable, its proximal portion is now about twice the size of its distal lobe, while in the stages previously described it is about half as large. The distal lobe is circular, the proximal wedge-shaped, with the small end proximal. Carpale II+III is the last carpale to chondrify, but is now all cartilage except a very small portion of its proximal end. It is an elongate mass, placed somewhat diagonally to the present axis of the limb. It is contiguous distally to the approximate surface of metacarpals II and III and carpale IV; proximally to the radiale. Carpale IV retains the same relative position as in earlier, except that it has approached closer to metacarpal III. Digits II and III have each added a segment, that of the former is partly cartilaginous, the latter is all procartilage. Metacarpal IV has approached metacarpal III and its single phalanx is entirely cartilaginous. Metacarpal V has the same appearance as in previous stages, but is farther from metacarpal IV.

Stage IV, (Fig. 4).

The specimen which forms the subject of this stage (fig. d) is in some respects slightly more developed than stage III, in

other respects less so. The manus is not flexed so much, and consequently the ulnare has not been pushed so far outside the ulna. In this specimen, unlike the others, the two lobes of the ulnare are about equal in size, the distal one oval, the proximal wedge-shaped. The radiale retains its bilobate appearance as described in stage I. Carpale II+III forms a lunate mass of fully developed cartilage about the head of metacarpal III. Carpale IV is slightly smaller relatively than in the previous stage; the digits are essentially the same.

STAGE V, (FIG. 5).

In the specimens (fig. e) which forms the basis of this stage, the manus now assumes very nearly the form which it has in the adult bird. The radiale is irregular in shape and fitted to the distal end of the radius, the inner distale margin of the ulna and the approximate surface of carpal II+III. The distal lobe of the ulnare is here at a minimum in comparison with the proximal lobe; it is now closely appressed to carpale IV which is wedged between it and carpale III. Metacarpal II has approached metacarpale III and on its radial side is developed a large projection or "trochanter." Its proximal phalanx is entirely cartilaginous, its distal one is just beginning to appear. Metacarpal III now bears three phalanges, the distal one not yet cartilaginous. Metacarpal IV has assumed a position parallel to metacarpal III, but is not yet united to it. Metacarpal V has approached metacarpal IV near its proximal end.

STAGE VI, (FIG. 6).

In birds of this age (fig. f), carpales II, III and IV have entirely coalesced, and, together with metacarpal II, form a solid socket into which fits the head of metacarpal III. Metacarpal II bears two phalanges; metacarpal III three, their distal phalanges being unequal. Metacarpal V now touches metacarpal IV and is not so near the proximal end as in earlier stages.

Stage VII, (Fig. 7).

There is little in this stage (fig. g) to note except metacarpal V. This is now an oval disk closely applied to the ulnar flexor surface of metacarpal IV, about one-ninth of the distance from the proximal to the distal end. It no doubt finally unites with metacarpal IV at that point.

Comparisons.

Intermedio-Radiale. In Sterna in the earlier stages these two elements are distinct (fig. 1); later they become so completely fused that they cannot be distinguished, although, exceptionally, (fig. 4) they partially retain their individuality for a considerable time. Similar conditions have been noted in several birds, *e. g.*, Opisthocomus, *Fulco tinnunculus* and chick by Parker and *Cypselus melba* by Zehntner ('90). In other birds the separation has not been described, possibly from the fact that the proper stages have not been studied.

Ulnare-Centrale. My observations here closely agree with those of Parker on the ducks and auks, there being the same tendency to subdivision of the cartilage mass into two elements which he shows. One of these is, beyond doubt the ulnare, but I confess I am not so certain of the other which I call centrale in deference to his better opinions. The conditions shown in fig. 1 where the two portions of this element are clearly shown, leads one to the conclusion that the distal lobe may possibly belong to the series of carpales, in which case it would be that of the fourth existing digit. In fig. 5 again the arrangement is such as to support such a view, while on the other hand, in none of the earlier specimens have I seen it in such a position as to indicate that it should be regarded as a centrale. In *Chloëphaga poliocephala* Parker ('90) describes this bone as divided into three portions, the two distal of which he terms centrale 1 and 2. It would rather seem as if we had here to do with a true centrale, while Parker's centrale 1—clearly, according to position, equivalent to the single one which I find—must be regarded as a fourth carpal. (Cf. Parker '90, pl. 5, fig. 14). Studer, according to the

single figure copied by Wiedersheim, has different ideas. He has no such projection from the ulnare, but in his figure carpale I+II projects np between radiale and ulnare and the projecting portion is the centrale. Zehntner, on the other hand, ('90) has the intermedium united to the ulnare, the centrale to the radiale, conditions which certainly do not occur in Sterna.

CARPALS. Unless we regard the "centrale" of the preceding paragraph as in reality a carpal, Sterna never possesses more than two distinct elements in the distal carpal series. Of these that on the radial side is the larger. When chondrification begins it occupies a position (fig. 2) at the base of metacarpal III; later (figs. 3, 4) it extends radially towards metacarpal II, and even at times (fig. 4) exhibits a marked bilobate appearance. From these facts as well as its subsequent history I regard it as a compound body, the carpales II+III of the normal pentadactyle hand, the distal carpal II of Parker and most other students of Avian osteology. Concerning the "pentosteon" of Shufeldt I can say little. This author ('82[b] p. 691, footnote) gives this name to a small bone found by him in Centrocercus lying at the base of the plantar surface of the second (my third) metacarpal. The name was given because it was the fifth carpal bone discovered, and because it was noncommittal as to its homologies. Parker now finds the same bone in ducks and auks, occupying the same position, and regards it as carpale I. This interpretation, however, seems to me faulty, as the bone is not in the proper position for such identification, nor have we any torsion or stress which could account for such translation. It would appear rather to belong to the same category as the pisiforme, but since I have not found it in Sterna I can offer no further observations upon it.

The other free carpal element, carpale IV, is clearly but a single element and not a compound structure like that described by Zehntner, Rosenberg and others. Studer, in the penguin, also figures a broad element in this position which he doubtfully regards as compound. In Sterna this element at its first differentiation is no wider than the fourth metacarpal, and as long as it retains its free condition it remains re-

latively of the same size. Later (fig. 6) it becomes united with carpale II+III, the whole forming a single piece equivalent to the separate os magnum and unciforme of some birds.

METACARPALS. The only metacarpal which requires notice is V (IV of many authors). This has been more or less perfectly described by several students since its first discovery by Rosenberg ('73). This author describes it in the chick as a distal process of a common mass of cartilage which clearly contains *two* carpal elements, IV+V, since to it is also joined metacarpal IV. In the case of his figures there can be no doubt that this distal prolongation is a true digital element, as it is clearly homonomous with the other metacarpals. It is to be noted that according to Rosenberg this new metacarpal lies at a lower level than the others, being flexed towards the palmar surface. Zehntner ('90) finds the same element in *Cypselus melba*, but existing there, as in Sterna, as a piece distinct from the basal (carpal) element with which it is at first joined in the chick. According to Zehntner after 9 or 10 days, this metacarpal "geht.... bei Cypselus einen vollständigen Atrophie." This is certainly not the case in Sterna, nor is it in those forms studied by Parker. Here it retains its discrete nature for sometime and in the fowl, toucan and cariama it even becomes ossified before its final union with the basal end of metacarpal IV.

That this is a true metacarpal is, I think beyond question. Owing to the method of study adopted by Parker he failed to recognize its earlier conditions, and his observations, unsupported by other evidence might be interpreted, as has been done by several, in another way. However, the evidence adduced by Rosenberg, Zehntner and myself, clearly removes this from the category of tendinous ossifications, the pisiforme and the like.

Naturally the structures which I have described should be compared with those of the reptiles, but this to be at all adequate would require a detailed knowledge far greater than I possess. It is to be noted, however, that if, as contended in the next section, the avian "pollex" is not the first digit of the pentadactyle hand, a portion of the reasons adduced for

regarding the Pterodactyls as widely removed from the birds is removed.

The Homologies of the Digits.

In the wing of the adult bird only three digits at most attain full development, and, since the birds have descended from pentadactyle forms, it becomes a matter of some importance to compare these three with those of the normal hand; in other words to ascertain which digits have been lost in the process of evolution. Naturally many attempts have been made to solve the problems involved, and within the last decade four different views have had their advocates, though naturally some of these ideas of homology date back to a more remote period.

Thus Gegenbaur ('64), reasoning from the apparent tendency towards reduction of the digital elements on the ulnar side of the crocodilian manus, concludes that the persistent digits of the bird wing are the I, II and III of the normal pentadactyle hand. In this he has had many followers, among them Rosenberg ('73), Huxley ('71), Jeffries ('81), Jackson ('88), and Parker ('88). For this view there are many more arguments than the one mentioned above, and Dr. Jeffries has given an able summary of them.

A second view is that of Owen, according to which the digits in question are II, III and IV. This is based partly ('36) on the fact of the absence of the radial artery, which would indicate reduction on the radial side of the manus; and partly ('62) on features supposed to exist in the British Museum specimen of Archæopteryx. In this there are apparently four digits present in connection with the right wing, but as these show considerable dislocation, one may, as suggested by Professor Owen, have belonged to the other side. This view has fewer supporters than the other, among them Morse and Coues. Morse ('72) contributes not a little in support by his advocacy of the law of digital reduction as a valid argument in this connection. That Coues supports the same view I take partly on the statement of others and partly from the fact that, while in the text of his "Key" ('87), he gives both views, the num-

bering of the digits is II, III, IV. In an earlier paper ('66) he accepts the numbering I, II and III. Here, too, must be enumerated Shufeldt, who states ('82, p. 616) that he has always adhered to this view, but adds "the fact, however, that the first phalanx of the manus of aves is the homologue of the pollex of the pentadactyle limb seems to be gaining ground." I have not found any further reference to this subject in his subsequent osteological contributions further than this usual reference to the radial digit as the pollex.

Mr. Hurst ('93) has advocated a third system of numbering according to which the digits are III, IV and V. An analysis of his reasons will be given immediately when dealing with the arguments for the enumeration adopted in the present paper.

The fourth system is that of Tschan ('89) who according to Zehntner ('90) proposes to regard the permanent digits as I, II and IV. He bases this on the discovery by Parker ('89) of a slip of bone in chick,[2] Musicapa and many Gallinæ as occurring between the second and third of the persisting digits. This, says Tschan, is the true digit III. But Parker further describes similar slips as occurring on the outside of the "pollex" and between the first and second permanent digits as well as a true fourth metacarpal on the ulnar side of the hand. Tschan suggests that the first of these might be the "prepollex" but even with the admission of this doubtful element, there would be one superfluous digit. This together with the utterly anomalous type of reduction which it presupposes—the disappearance of digits in the middle of the manus—is sufficient to discredit this view.

That there is developed a fourth digit in the avian manus is beyond question, and the fact that this comes upon the ulnar side of the three permanent fingers is sufficient to invalidate the nomenclature, III, IV and V of Hurst. Hurst refers to Parker's fourth digit as appearing to be the *os pisiforme*, and since Parker had only the later stages, there would be some plausibility in this view. This possibility, however, disappears

[2]It was discovered, as Parker points out, long before by Heusinger ('20, pl. IV f. 10) in the chick, persisting for sometime as a separate bone.

when we study not only my figures 1 and 2, but the figures of Rosenberg and Zehntner. In the figures just cited the temporary digit is just as prominent as is the "pollex" and no one without a theory to support would regard it other than a digit. Then too, as Rosenberg's figure shows, it bears no connection to the ulnare, but is a distinct outgrowth from the outer distal angle of carpal III+IV.

We are then left to choose between the formulæ I, II and III and II, III, IV, and though the apparent weight of authority is in the other direction, I am strongly inclined towards the second alternative, for the following reasons: First comes the law of digital reduction advocated by Morse, by which in other groups digit I is first to disappear and then V. Further, when further reduction occurs in birds, and a single digit is left as in the Apteryx and the Cassowaries, the reduction has occurred on both sides of the persisting digit, which, according to my nomenclature, would be digit III. This implies a symmetrical reduction, the other view involves the disappearance of digits I, III, IV and V, a condition, so far as I am aware, without parallel.

Then too, Archaeopteryx, in the light of Hurst's later studies presents some evidence. As noted above, Owen thought he had found evidence of a true digit I in the British Museum specimen, but on the discovery of the Berlin specimen this idea was dropped and the conditions presented by the new example form the chief argument in Jeffries' summary already alluded to. It would, however, appear that most recent figures of the Berlin specimen and the conclusions based upon them are not to be relied upon. This can be at once seen by comparing for instance the figure of Archaeopteryx given by Zittel in his Paleontologie with the photographic reproduction which illustrates Hurst's article.[3] In the Berlin specimen three digits in the wing are clearly visible, and it has been assumed that these were the only ones. Hurst, however, points out that the position of the feathers is such that they could not have been borne on these digits as in ordinary birds,

[3]The plate in the Standard Natural History (Vol. IV, facing p. 22, 1885) approaches very closely the figure of Hurst.

but that there must be (at least one) digits buried beneath the feathers, and in just the place where the missing finger or fingers should come is an evident ridge in the stone.

If we may call upon the effects of use and disuse, the conditions presented would also tend to favor the reduction of the digits on the radial side, for it is the ulnar phalanges which must bear the stress of the wing; the fingers on the radial side, having but few small feathers, would be most likely to disappear.

Jeffries invokes also the distribution of the nerves, but to my mind his evidence is not conclusive; besides it is directly negatived by the distribution of the blood vessels as was pointed out above.

We may conclude, then, that the only conditions possible are either I, II and III, or II, III and IV, and that until some evidence be found of the actual appearance of a fifth digit on the ulnar side, that there is at least as much reason for the second as for the first formula. In regard to the first, Hurst remarks, it "is in no case, so far as I am aware, supported by any evidence whatever. I believe it to have originated from the pre-Darwinian statement that the Ala spuria is 'analogous to the thumb;' while the other two digits are called simply 'second' and 'third;' that is, *second and third digits* not of the pentadactyle but *of the tridactyle fore-limb.* Such phrases written on the then undoubted hypothesis of special creation and of fixity of species, could obviously not mean that the three digits called 'thumb' and 'second' and 'third' had been evolved from the digits I, II, III of the pentadactyle fore-limb of an ancestor; the author did not believe that birds ever had such an ancestor. The transcription of such phrases into post-Darwinian treatises, without consideration of the new meaning which they would thus gain from the new context, appears to have been the origin of the error."

Conclusions.

Carpals. There are at least seven elements in the carpus. In the proximal row there are two free elements (intermedio-radiale and centralo-ulnare) both of which are divided in the

early embryo, and represent, morphologically, the radiale, intermedium, centrale and ulnare. In the distal series there are also two free elements, one of them (carpal II+III) being evidently compound.

DIGITS. There are four distinct metacarpals. The first (II) supports two phalanges, the second three, the third one, and the fourth none. The distal phalanges of m. c. II and III are furnished with claws. *M. C.* V arises as a distinct digit, subsequently becomes free, and finally unites with m. c. IV.

NUMBERING OF DIGITS. The persistent digits of the birds wing are either I, II and III or II, III and IV, the bulk of evidence being in favor of the latter enumeration.

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Explanation of the Figures.

The illustrations in the text show the embryos natural size. It is to be noted that fig. A, showing a smaller embryo, had a wing more developed than fig. B. All other figures are projections of camera drawings and are each magnified 22 diameters.

REFERENCE LETTERS.

c carpale	*m. c.* metacarpal.
h humerus	*u* ulna.
r radius	*ue* ulnare.
re radiale	II–IV and I–IV digits.

Fig. 1. Manus, stage I, showing carpus and digits as procartilage with several cartilaginous elements. Digit V is plainly shown.

Fig. 2. Manus, stage II. Three carpals are now seen and metacarpal V has become distinct from the carpal mass.

Fig. 3. Manus, stage III. The digits are now broken into phalanges and the flexure of the hand to the ulnar side is forcing the ulnare out of its normal position.

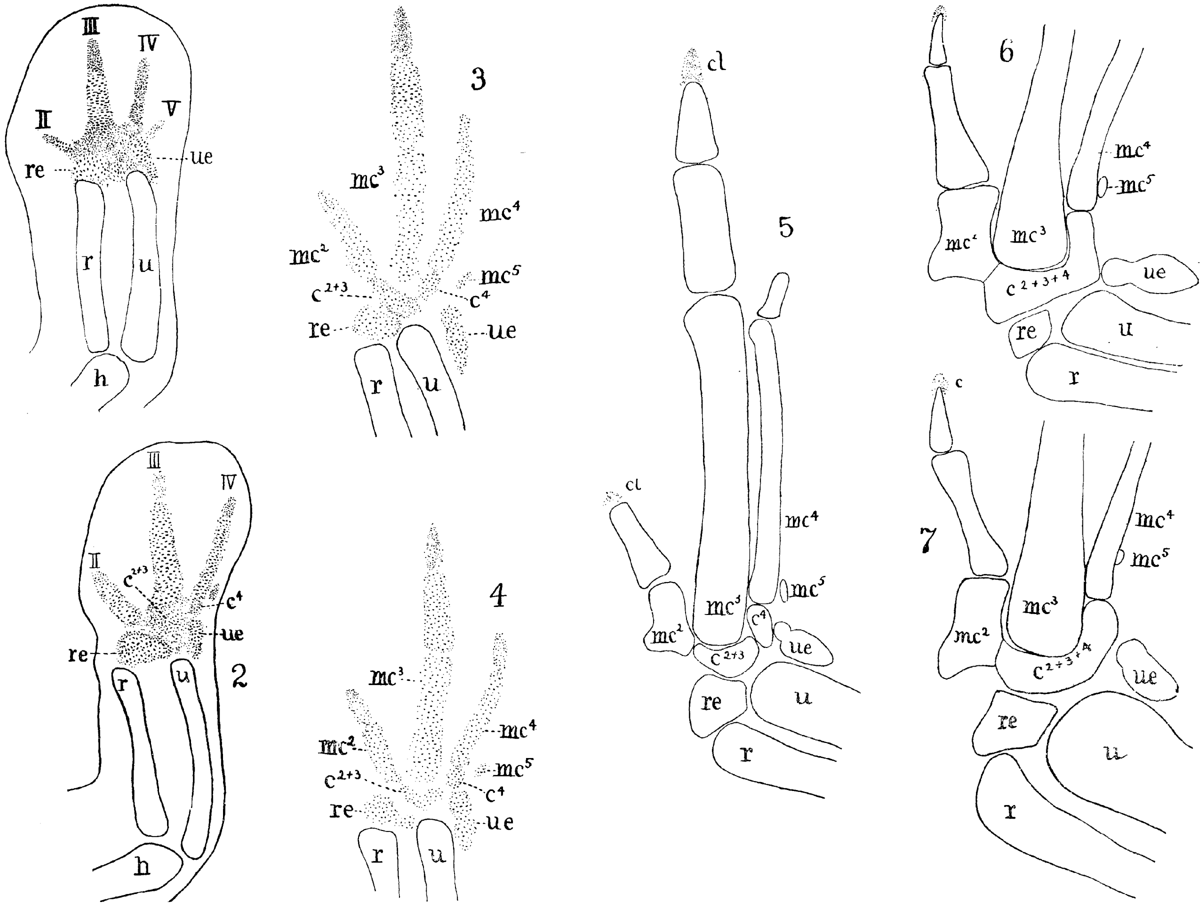
Fig. 4. Manus, stage IV. The radiale shows tendency to division into radiale and intermedium.

Fig. 5. Manus, stage V. Elements now beginning to ossify. Digits II and III are terminated with claws.

Fig. 6. Carpals and metacarpals, stage VI. Carpals united; metacarpal V approximate to metacarpal IV.

Fig. 7. Conditions just before hatching. Metacarpal V joined to metacarpal IV.

PLATE XXV.



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